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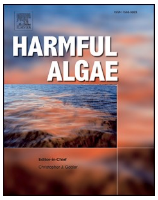

Original Article

Research on the biology and ecology of the harmful algal bloom species *Phaeocystis globosa* in China: Progresses in the last 20 years

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ABSTRACT

Chinese researchers have made substantial progresses in research on the harmful algal bloom (HAB) species *Phaeocystis globosa* since the first *P. globosa* bloom outbreak in the Chinese coastal waters in 1997. However, as many results, especially the earlier ones, were published in non-English literature, much of the research on *P. globosa* biology, ecology, and biogeochemistry made by Chinese researchers have been unknown to colleagues from other countries. We review current knowledge on taxonomy, morphology, genetics, physiology, survival strategies and mitigation of *P. globosa* gained by Chinese researchers from the past two decades. *P. globosa* is the only *Phaeocystis* species that causes blooms in the Chinese waters, although other *Phaeocystis* species including *P. jahnii* and *P. cordata* have been detected in Chinese coastal regions. *P. globosa* has a complex life history with at least two morphotypes including a haploid flagellate and a diploid colonial cell. Colonial *P. globosa* blooms typically occur in winter after a diatom bloom in coastal waters of the South China Sea. *P. globosa* in Chinese coastal waters usually has extremely large colonial sizes, up to 3 cm in diameter, an order of magnitude greater than that observed in European coastal waters. The development of giant colonies is associated with enhanced sinking rate, limited nutrient diffusion, as well as decreased stability of colonies. The Chinese *P. globosa* strains also showed strong genetic diversity and physiological plasticity, being able to grow and develop into colonies at higher temperature and irradiance relative to that in European waters. High genetic diversity of *P. globosa* was revealed by developing high-resolution and high-specificity molecular markers including *Phaeocystis globosa* chloroplast 1 (*pgcp1*). Due to the severe impact of *P. globosa* on ecology and economy, much effort has been made to mitigate *P. globosa* blooms including the application of modified clays. Overall, *P. globosa* in the Chinese waters demonstrate unique genetic, phenotypical and physiological features that differ from *P. globosa* in other ocean regions. Further studies are needed to explore how environmental factors trigger the occurrence of *P. globosa* blooms and ascertain the impact of *P. globosa* blooms on the environment.

1. Introduction

Phaeocystis (Prymneisophyceae) is a marine phytoplankton genus with worldwide distribution and plays an important role in climate changes, including the cycles of carbon, sulphur and trophic structure (Lancelot et al., 1998; Peperzak et al., 1998; Smith et al., 1991). It has a complex polymorphic life cycle alternating between solitary free-living cells and colonies. Solitary cells, either flagellated or non-flagellated, are generally 3–10 μm in diameter, whereas colonies are composed of cells embedded within a mucilaginous envelop. The colonies are filled with fluid internally and can reach up to 3 cm in diameters (Rousseau et al., 1994; 2007; Qi et al., 2004). Among the seven *Phaeocystis* species that have been described (Medlin and Zingone 2007; Anderson et al., 2015), three species *P. globosa, P. pouchetii* and *P. antarctica* are known to form dense blooms of gelatinous colonies (Lancelot et al., 1998; Schoemann et al 2005; Smith et al., 2014a). *Phaeocystis globosa* has been regarded as a harmful algal species due to the negative impacts on local marine ecosystems and human activities (Lancelot et al., 1998; Schoemann et al., 2005).

The first occurrence of *P. globosa* blooms in China was recorded in

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1997 (Qi et al., 2004). Since then, *P. globosa* blooms regularly occur in Chinese coastal waters. To better understand mechanisms underlying survival and growth of *P. globosa*, substantial efforts have been made to address questions regarding taxonomy, morphology, and abiotic and biological factors that are responsible for the growth and colony formation of *P. globosa* (Chen et al., 1999; Xu et al., 2003; Wang et al., 2007; Hu et al., 2019a). Some of these findings are dramatically different from those of other studies of *P. globosa* (Lancelot et al., 1998; Peperzak et al., 1998; Schoemann et al., 2005; Rousseau et al., 2007), which may reflect genetic differences among *P. globosa* strains identified in different regions. These studies could have been an important complement to the understanding of *P. globosa* ecology and biogeochemistry. However, as many of these researches were published in Chinese journal, much of the results were unknown to researches in other countries.

In this review article, we summarize the current knowledge on biology and ecology of *P. globosa* in Chinese waters primarily by Chinese researchers. Since *Phaeocystis* was described by Lagerheim in 1893, there have been over 10 reviews on ecophysiology of *P. globosa* (Riegman and Boekel 1996; Schoemann et al., 2005; Vogt et al., 2012)(also see Journal of Marine Systems, volume 5(1), 1994 and Biogeochemistry, volume 83, 2007). We highlight the unique characters associated with *P. globosa* in Chinese waters, with emphasis on those findings in the past 20 years. The knowledge gained by Chinese researchers should be valuable in understanding the ecology and biogeochemistry of *P. globosa* strains in the Chinese coastal waters.

2. A brief history of *P. globosa* blooms in China

1997-1998 was an unusual period of time in China, as many HABs occurred in the coastal waters of the South China Sea. Among 13 HABs events described (Qi et al., 2004), *P. globosa* blooms drew the most attention, not only due to the economic losses caused by the blooms, but also the unique biological and ecological characters exhibited by *P. globosa*. In October 1997, the first *P. globosa* bloom was observed in Quanzhou Bay, followed by rapid expansion southward to the South China Sea (**Fig. 1**). One month later, massive blooms of *P. globosa* colonies were observed in Zhelin Bay, which was described as “red bubbles” by local fishermen, although colonies appeared to be brown or yellow (Huang et al., 1999; Chen et al., 1999). *P. globosa* blooms eventually vanished at the end of February 1998, when white foams with strong unpleasant odors accumulated on ocean surface and the beaches due to degradation of colonial materials (Qi et al., 2004; Xu et al., 2003). Since then, *P. globosa* blooms were reported at least once per year in the Chinese coastal waters (Wang et al., 2007; Dou et al., 2015; Table 1). Most *P. globosa* blooms occurred in the tropical waters of the South China Sea (Chen et al., 1999; Xu et al., 2015), but some also occurred in temperate estuaries and coastal waters including the Bohai Sea and East China Sea (Qu et al., 2008; Tu et al., 2011; Xing et al., 2017; **Fig. 1 and Table 1**).

P. globosa blooms usually occur after diatom blooms in winter to early spring in the South China Sea (Table 1), although blooms have also been observed in summer and autumn in Guangdong, Guangxi and Hainan coastal waters (Xu et al., 2003; Liu et al., 2008; Li et al., 2012). For example, diatoms appeared to be the lowest in cell abundance in summer in the Beibu Gulf, but became dominant in fall and winter (Jiang et al 2012; Wang et al., 2015). Diatoms were mainly composed by chain-forming species including *Chaetoceros* sp., *Rhizosolenia* sp., *Thalassionema* sp., *Skeletonema* sp., and *Pseudo-nitzschia pungens* (Jiang et al., 2012; He et al., 2019). *P. globosa* colonies were observed in December (He et al., 2019), and develop blooms in January-February (Li et al., 2015; He et al., 2019). Colonial *P. globosa* blooms disappeared in March, while chain-forming diatoms become dominant again (Jiang et al.,

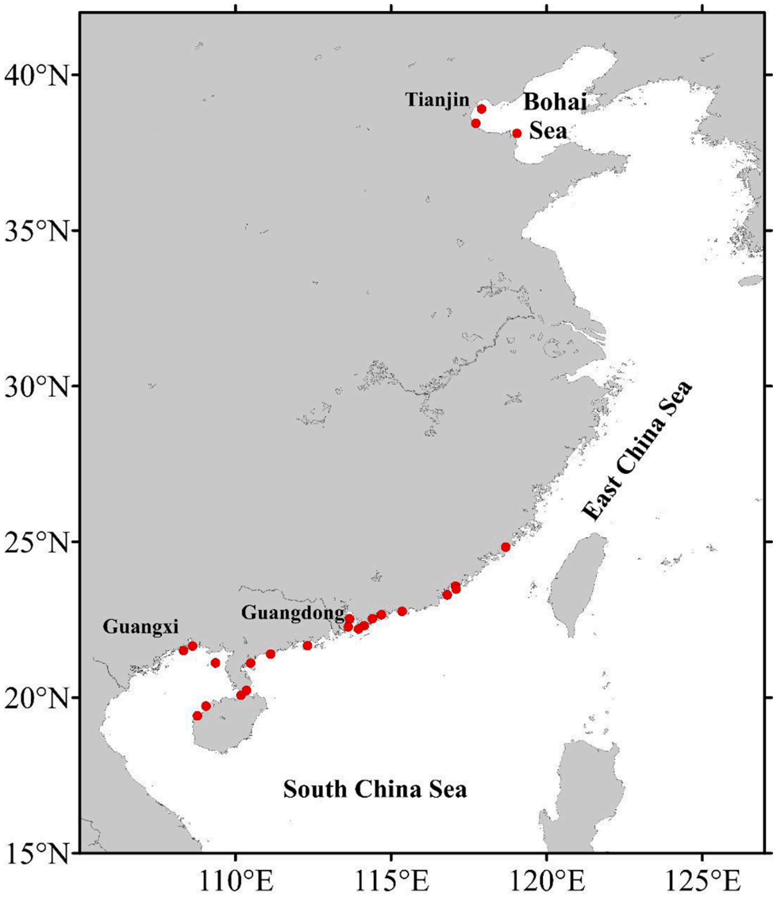

Fig. 1. The distribution of *Phaeocystis globosa* in the Chinese waters.

Table 1
Date, location, effects of some *P. globosa* blooms as well as water temperature, nutrient and maximum colony abundances during blooms reported in coastal waters of the China Sea (n.d. no data available).

Date	Location	Effects	Temperature (°C)	Nitrate (μmol L^{-1})	Phosphate (μmol L^{-1})	Maximum N_{Colony}(Colonies L^{-1})	Reference
	Bohai Sea						
Jun. 2004	Yellow river estuary	n.d.	n.d.	n.d.	n.d.	n.d.	Bulletin of China Marine Disaster (2004)
Jun. 2005	Bohai Bay	n.d.	n.d.	n.d.	n.d.	n.d.	Bulletin of China Marine Disaster (2005)
Jul.-Aug. 2005	Yellow river estuary	Killing of fishes	n.d.	n.d.	n.d.	n.d.	Bulletin of China Marine Disaster (2005)
Oct. 2006	Tianjin coast	n. d.	16-20.8	3-56	0.16-1.1	n.d.	Bulletin of China Marine Disaster (2006); Tu et al. (2011)
Oct. 2006	Hebei coast	Killing of shrimp	n.d.	n.d.	n.d.	n.d.	Bulletin of China Marine Disaster (2006)
	East China Sea						
Oct. 1997	Quanzhou Bay	Killing of fishes	25	n.d	n.d	n.d	Huang et al. (1999); Chen et al. (1999)
Sep. 2015	Quanzhou Bay	n.d.	n.d.	n.d.	n.d.	n.d.	Bulletin of China Marine Disaster (2015)
	South China Sea						
Dec. 1997-Jan. 1998	Zhelin Bay	Killing of fishes	17.7-20.5	4.2-9.5	0.36-0.647	282	Huang et al. (1999); Xu et al. (2003)
Jul. 1999	Zhelin Bay	n.d.	25-26	n.d.	n.d.	n.d.	Xu et al. (2003)
Feb. 2000	Hainan coast	n.d.	n.d.	n.d.	n.d.	n.d.	Li et al. (2012)
Feb. 2002	Hainan coast	n.d.	n.d.	n.d.	n.d.	n.d.	Li et al. (2012)
Dec. 2002	Hongkong coast	n.d.	n.d.	n.d.	n.d.	n.d.	Li et al. (2012)
Jan. 2003	Shantou coast	n.d.	n.d.	n.d.	n.d.	n.d.	Li et al. (2012)
Aug. 2003	Zhelin Bay	Killing of fishes	n.d.	n.d.	n.d.	n.d.	Li et al. (2012)
Dec. 2003	Pearl River Estuary	Killing of fishes	n.d.	n.d.	n.d.	n.d.	Li et al. (2012)
Jan. 2005	Zhanjiang port	n.d.	n.d.	n.d.	n.d.	n.d.	Li et al. (2012)
Feb. 2006	Zhuhai coast	n.d.	n.d.	n.d.	n.d.	n.d.	Li et al. (2012)
Apr. 2006	Haikou coast	n.d.	n.d.	n.d.	n.d.	n.d.	Li et al. (2012)
Aug.-Oct. 2006	Weizhou Island	n.d.	27.2-30.0	2.93-6	0.03-0.16	n.d.	Liu et al. (2008)
Dec. 2006	Shanwei port	n.d.	n.d.	n.d.	n.d.	n.d.	Bulletin of China Marine Disaster (2006)
Feb. 2007	Shantou Bay	Killing of scallop	15-18	n.d.	n.d.	3-5	Zhao et al. (2009)
Sep. 2007	Shanwei Port	n.d.	n.d.	n.d.	n.d.	n.d.	Bulletin of China Marine Disaster (2007)
Nov.-Dec. 2009	Pearl River Estuary	n.d.	19.04-21.5	n.d.	n.d.	6	Wang et al. (2010)
Dec. 2009	Northwest Hainan Island	n.d.	n.d.	n.d.	n.d.	n.d.	Li et al. (2012)
Jan. 2013	Northwest Hainan Island	n.d.	~20	0.28-19.8	0.03-0.61	n.d.	Xu et al. (2015)
Feb.-Mar. 2014	Beibu Gulf	Clog nuclear plant	17.3-20.5	14.28-21.7	0.97-0.45	30	Li et al. 2015
Dec. 2014-Feb. 2015	Beibu Gulf	Clog nuclear plant	n.d.	n.d.	n.d.	n.d.	Hu et al. (2019b)
Jan.-Feb. 2015	Northwest Hainan Island	n.d.	n.d.	n.d.	n.d.	n.d.	Bulletin of China Marine Disaster (2015)
Jan.- Feb. 2016	Beibu Gulf	Clog nuclear plant	19.3-22.7	6-17.25	0.34-1	41	He et al. (2019); Yuan et al. (2019)
Feb. 2017	Maoming coast	n.d.	n.d.	n.d.	n.d.	n.d.	Bulletin of China Marine Disaster (2017)
Mar. 2017	Zhanjiang Bay	n.d.	n.d.	n.d.	n.d.	n.d.	Bulletin of China Marine Disaster (2017)

2012; He et al., 2019). These observations were consistent to previous observations on the occurrence of *P. globosa* blooms in the North Sea in Europe, which occurred after spring diatom blooms (Lancelot et al., 1998; 2007; Peperzak et al., 1998; Rousseau et al., 2002; Breton et al., 2006). Similar trend in phytoplankton succession in the coastal waters of high latitude North Sea in Europe and tropical South China Sea suggested that the blooms of diatoms/*Phaeocystis* are likely to be regulated by similar environmental factors. The occurrence of diatom/*Phaeocystis* blooms in the North Sea can be generally explained by high anthropogenic nutrient enrichment and shift in nutrient ratios (Lancelot et al., 2007). In general, diatom blooms occur when nutrients are sufficient, *P. globosa* blooms occur after Si is depleted by diatoms (Lancelot et al., 1998; Rousseau et al., 2002). The water mass of coastal waters of the South China Sea are also largely influenced by excessive nutrients load due to freshwater input and agriculture fertilizer (Huang et al., 2003; Chen and Chen 2006; Qiu et al., 2010). During 1970-2000, dissolved N and P inputs to the coastal seas of China increased by a factor of 2-5 (Strokal et al., 2015), resulting in the decreased ratios of Si to N and P. In the Beibu Gulf, nitrate and phosphate concentrations were up to 13 and 1.3 μmol L^{-1}, respectively, throughout the whole years (Yuan et al., 2019). Excess nutrient input could be one of the triggers for *P. globosa* blooms in Chinese waters. However, studies on relationship between nutrient available and *P. globosa* blooms are still limited (Table 1).

P. globosa blooms in the Chinese coastal waters are characterized by giant colony sizes and high biomass, which are generally associated with massive economic loss. Colonies were generally 1–2 cm in diameter (**Fig. 2**), while colonies of up to 3 cm were occasionally observed (Chen et al., 1999; Qi et al., 2004). These colonies are at least an order of magnitude larger than those from the North, East Greenland and Ross Seas (Hamm et al., 1999; Smith et al., 2003; Rousseau et al., 2007; Verity et al., 2007). *P. globosa* colony abundances generally ranged from several to several hundred colonies L^{-1} (He et al., 2019; Li et al., 2015), with cell abundances ranging from 10^6 to 10^7 cells L^{-1} during blooms (Chen et al., 1999; Xu et al., 2003; Li et al., 2015). The maximum colony abundance of 282 colonies L^{-1} was observed in the South China Sea in September 1998, resulting in cell abundance of 2.5×10^8 cells L^{-1} (Huang et al., 1999). This biomass is comparable with those reported in the North Sea during a bloom of *P. globosa* colonies in May 1985 (2.0×10^8 cells L^{-1}; Cadée and Hegeman, 1986).

The occurrence of blooms caused by giant colonies usually resulted in the massive local economic loss. For example, the long-lived *P. globosa* blooms in Zhelin Bay in 1998 caused mass mortality of fish in aquaculture cages, resulting in estimated loss of about 7.5 million dollars to the local economy (Chen et al., 1999; Qi et al., 2004). *P. globosa* blooms are responsible for the mortality of scallops resulted in loss of 0.5 million US dollars in Shantou waters in February 2007 (Zhao et al., 2009). In 2015, giant colonies clogged cooling water outlet of nuclear power plant in the Beibu Gulf, Guangxi province, threatening its operational safety (He et al., 2019). Despite the negative impacts on economic development and human activities, occurrences of *P. globosa* blooms in Chinese coastal waters also provide a valuable opportunity to assess the biology and ecology of *Phaeocystis*.

3. Taxonomy of *P. globosa*

Over the past two decades, at least six *Phaeocystis* species have been described based on sequence variations in the 18S rRNA genes, which are cluster into three clades. *P. jahnii*, which is a unicellular species, represents the earliest clade; *P. cordata*, which is another unicellular species, represents the next branching clade; *P. rex* (unicellular species) and three colony-forming species, *P. globosa, P. antarctica,* and *P. pouchetii* together form the largest clade. Lange *et al.* (2002) suggested that 18S rRNA can only resolve major species complexes, as little divergence was seen among the multiple isolates sequenced from three colonial species. Despite only a few molecular phylogenetic studies of *P. globosa* strains collected from China seas have been carried out (Hu et al., 2019b; Qin et al., 2016; Qu et al., 2008; Wang et al., 2000; Xu et al., 2020), all the results consistently demonstrated that *P. globosa* is the only causative species of *Phaeocystis* bloom in Chinese waters. In other words, *P. antarctica* and *P. pouchetii* have not been identified in blooms in Chinese waters.

Through metabarcoding analysis using 18S rDNA V4 region, we identified the presence of *P. globosa* in the Jiaozhou Bay (Liu et al., 2020), although *P. globosa* blooms have not been reported in the Jiaozhou Bay, consistent with the wide distribution patterns of *P. globosa*, suggesting that the wide existence of *P. globosa* in Chinese waters. *Phaeocystis* species other than *P. globosa* have also been observed in the Chinese waters, primarily through molecular analysis. For example, *P. jahnii* (PID ranged from 98.5% to 99.4%) and *P. cordata* (PID ranged from 97.8% to 98.1%) were identified through sequencing 18S rDNA gene sequences in the East China Sea (Lin et al., 2014; Shih et al., 2019). In the latter study, three *Phaeocystis* species, including *P. globosa, P. cordata*, and *P. jahnii*, were identified in the same samples as top-ranking species (Shih et al., 2019), suggesting biological diversity of *Phaeocystis* species in the Chinese coastal waters. However, *P. jahnii* and *P. cordata* strains have not been isolated in Chinese waters, likely due to their small sizes. Successful isolation and culturing of these species would facilitate research on the biology and ecology of these *Phaeocystis* species.

4. Genome analysis of *P. globosa*

Although the Joint Genome Institute of the USA initiated the *P. globosa* genome project (https://jgi.doe.gov/why-sequence-phaeocystis-globosa/), by now no *P. globosa* genome assembly has been published. The lack of a reference genome of *P. globosa* hinders research towards understanding the biology and ecology of *P. globosa* and mechanisms underlying the formation of *P. globosa* blooms.

The chloroplast genome (cpDNA) of *P. globosa* strain CNS00067, which was isolated from the Beibu Gulf in the South China Sea, was recently constructed (Song et al., 2020). This CNS00067 cpDNA was 106,419 bp in size, which was slightly smaller than that of the strain Pg-G(A) that (107,461 bp) was isolated from the North Sea of Europe (Smith et al., 2014b). The CNS00067 cpDNA contains 141 genes including 108 protein-coding genes, three rRNA genes and 27 tRNA genes. In the *P. globosa* CNS00067 cpDNA, each of the two IR regions was found to contain three rRNA genes (*rrnL, rrnS* and *rrn5*), while IRb was slightly larger than IRa, with two additional tRNA genes (*trnI* and

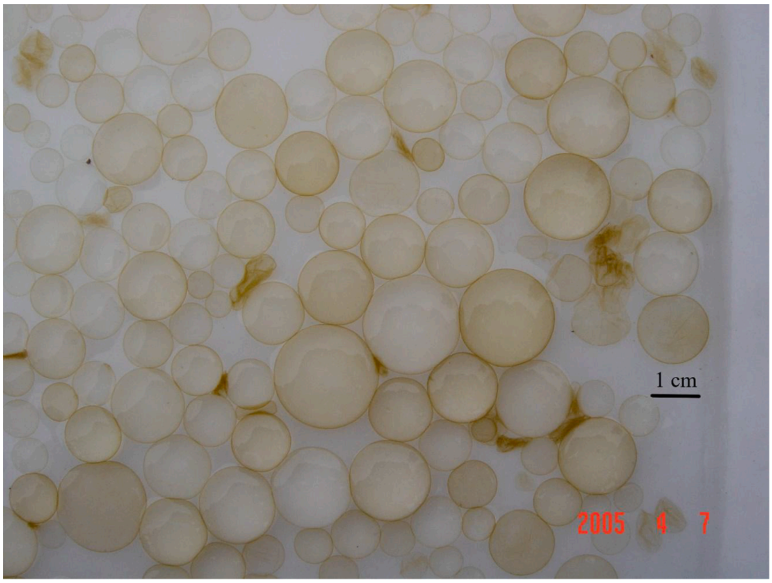

Fig. 2. Giant colonies collected from coastal waters of the South China Sea in 2005 when *P. globosa* bloom was observed. Bar =1 cm.

trnA). The CNS00067 cpDNA encoded all genes found in other 11 strians and *P. globosa* strain Pg-G(A) NC_021637, the percent identity was 98.2%–100% and genes are strongly conserved (Song et al., 2020).

The mitochondrial genome (mtDNA) of *P. globosa* proved to be complex with extremely long repeat regions that was hard to resolve. The mtDNA of the strain Pg-G(A) was partially complete with one repeat regions unresolved (Smith et al., 2014b). Recently, using the long read DNA sequencing technology PacBio Sequel II, we successfully constructed the complete mtDNA of the Beibu Gulf strain CNS00066. This genome, which was 43,585 bp in size, has two large repeat regions, 6.7 Kb and ~14 Kb in sizes, was completely resolved (Song et al., 2021b, in press).

5. Genetic diversity of *P. globosa*

Multiple lines of evidence suggest that *P. globosa* has high genetic diversity, and that different *P. globosa* strains may have differential contribution to the development of *P. globosa* blooms. It has been reported that *P. globosa* strains in different geographical regions may have differential level of toxicity (Wei and Jiang, 2005), optimal growth temperature (Shen et al., 2000; Wang et al., 2003), colonial sizes (Liang et al., 2020; Shen et al., 2018) and cell surface structures (Hu et al., 2019a), further suggesting that *P. globosa* strains have diverse genetic backgrounds.

Common molecular markers that can be applied to distinguish *Phaeocystis* species do not have adequate resolution for distinguishing *P. globosa* strains. For example, 18S rDNA was found to only resolve major species complexes (Lange et al., 2002). 28S rDNA D1-D2 sequence was found to have substantial intra-strain sequence diversity (Hu et al., 2019b). ITS1 was found to exhibit extremely high intra-genome sequence variations and therefore does not accurately represent the true phylogeny and obscures phylogenetic relationships (Medlin and Zingone, 2007; Hu et al. 2019b). To study the roles that different *P. globosa* strains play in bloom development, high resolution molecular markers that can adequately distinguish different *P. globosa* strains need to be developed.

Chloroplast is a vital and semiautonomous organelle, and many molecular markers have been developed based on the chloroplast DNA (cpDNA). Recently, we constructed a high-resolution molecular marker for distinguishing different *P. globosa* strains through comparative analysis of *P. globosa* chloroplast genomes using the chloroplast genome of the *P. globosa* strain CNS00067 as reference. The molecular marker *pgcp1* (*Phaeocystis globosa* chloroplast 1) was successfully used to separate *P. globosa* strains into at least four unique clades, three of which could be further divided into multiple subclades (Song et al., 2020). Compared to the molecular marker *rbc*S-*rpl*27 intergenic spacer developed and applied recently (Zhang et al., 2020a), *pgcp1* has been found to have higher resolution that can identify more genetic clades of *P. globosa* (Song et al., 2020).

Taking advantage of the mtDNA of *P. globosa* (Song et al., 2021b, in press), we analyzed *P. globosa* genetic variations using the *COX1* gene as the molecular marker (Song et al., 2021a, in press). Genetic diversity revealed by these two new molecular markers *pgcp1* and *COX1* were similar but complementary, suggesting that these two molecular markers may have different mutation rates, and that these two molecular markers, which were from two different organelles, represent different evolutionary trajectories.

6. Transcriptomics analysis of *P. globosa* colonial formation

Transition from the free-living solitary morphotype to the colonial morphotype is a hallmark in the development of *P. globosa* blooms. However, mechanisms of this transition remain poorly understood. Recently, Zhang et al. (2020b) explored the mechanisms by comparing gene expression of *P. globosa* cells at four distinctive stages: free-living solitary cells, two-cell-, four-cell- and multi-cell colonies using the RNA-Seq approach. The result showed that Glycosaminoglycan (GAG) synthesis and the synthesis of GAG precursors were enhanced while the degradation of GAG was decreased during the colony formation. They also identified decreased cell defense and motility, which might be important to save energy for GAG biosynthesis. They concluded that temperature was a critical factor regulating colony formation through mediating the intracellular accumulation of GAGs (Zhang et al., 2020b).

7. Morphology of *P. globosa*

Only one study analyzed morphotypes occurring within *P. globosa* from coastal waters of the South China Sea (Hu et al., 2019a). Two cell types of *P. globosa* (flagellates and colonial cells) have been described using light microscopy, scanning electron microscopy and flow cytometry.

7.1. *Haploid flagellate*

Flagellates are round and are 2.3–4.0 μm in diameters (Hu et al., 2019a; **Fig. 3**: A, B), which are smaller than *P. globosa* flagellates described in the North Sea (3–5.8 μm, Rousseau et al., 2007). It possesses two flagella and a haptonema. The flagella are 4.8–9.9 μm in length, while the haptonema is 1.5–2.1 μm in length (**Fig. 3**: A). Cell surface is covered by round organic scales (**Fig. 3**: A, B). Flagellated cells release filaments, forming a pentagonal star (**Fig. 3**: C). A remarkable feature of flagellated cells is that cell surface was covered by 2 circular bulges (**Fig. 3**: A, B; Hu et al., 2019a), which were not previously observed for *Phaeocystis*. Flagellate cells are haploid (Hu et al., 2019a).

7.2. *Colonial cells*

Colonial cells are generally spherical, and evenly distributed within a mucilaginous matrix. Colonial cells are 3.7–6.6 μm (Hu et al., 2019a), smaller than colonial cells of *P. globosa* reported from the North Sea (4.6–10.4 μm; Rousseau et al., 2007). Colonial cells possess two short appendages of 0.2 μm long (**Fig. 3**: D), but do not have flagella, star-forming filaments and scale covering. Colonial cells are diploid (Hu et al., 2019a). Hundred thousand of cells were distributed evenly within the gelatinous matrix and protected by an elastic membrane (Smith et al., 2014a). Colonies are typically 0.25–3 cm in the field (Chen et al., 1999; Smith et al., 2014a; Fig. 2), but are 10–1000 μm in the culture (Wang et al., 2014; 2015). Colonies maintained a spherical shape in seawater, but became flattened when removed from their environment. The colony envelop was slimy, elastic, and tough and was ca. 50 μm in thickness (Smith et al., 2014a), which is thicker than those of strains in the North Sea (<1 μm Hamm et al., 1999). The colors of giant colonies varied from bisque to brown, but were not correlated with colony size (Smith et al., 2014a);.

8. Giantism and its roles in survival and growth

Size is a major component of functional traits for phytoplankton ;) (Finkel et al., 2010; Litchman et al., 2007; Sommer et al., 2017), as it affects crucial physiological and ecological processes, including nutrient uptake, photosynthesis, respiration, growth, sinking and grazing (Key et al., 2010; Ward et al., 2011; Finkel, 2001; Bienfang and Harrison 1984; Marañón, 2015). Large size can also bring challenges for survival and growth of *P. globosa* in terms of fragile colony envelope, nutrient diffusive limitation, enhanced sinking rates and reduced growth rates ; ; (Jakobsen and Tang, 2002; Ploug et al., 1999a; Smith et al., 2014a; Wang et al., 2014). Giant colonies of *P. globosa* of tropical coastal waters showed some eco-physiological characteristics that are substantially different from those found in temperate oceans (Smith et al., 2014a), suggesting that *P. globosa* strains found in different regions may be genetically different, which is supported by genetic analysis using the newly developed molecular marker *pgcp1* (Song et al., 2020).

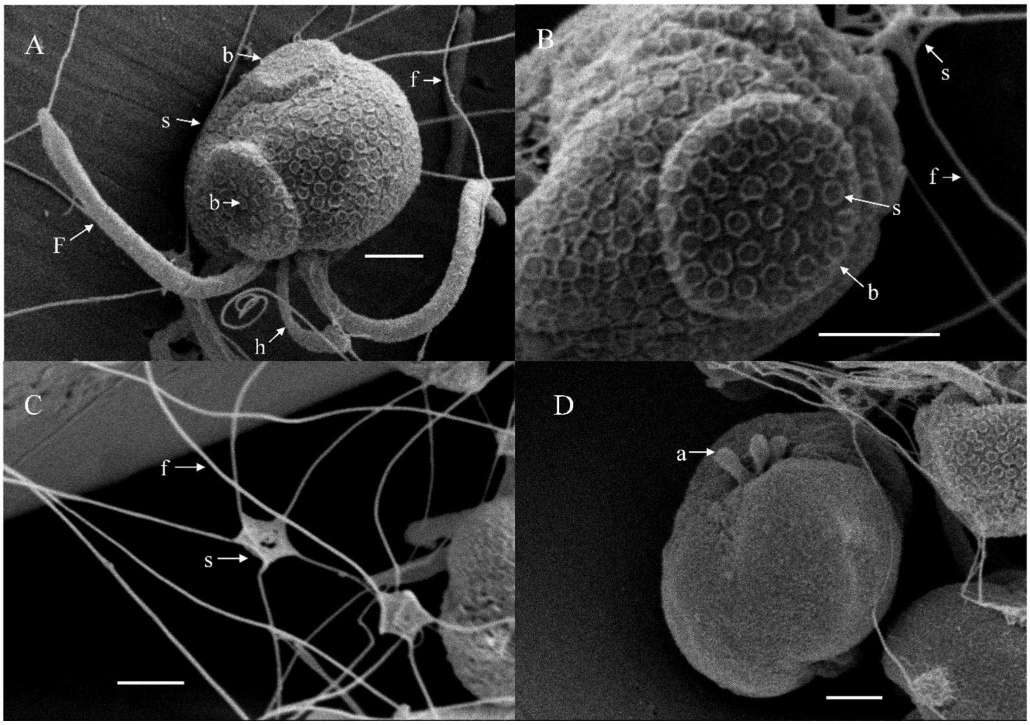

Fig. 3. SEM photographs for *P. globosa* cells observed in the coastal waters of South China Sea. (A): a flagellate bearing two flagella (F), a haptonema (h), two circular bulge (b), and scales (s) covering cell surface; (B): filaments (f), circular bulge (b) and scales (s) of flagellate; (C) pentagonal star (s) structure by filaments (f) released by flagellate; (D): a colonial cell with the short appendages (a). Bar=1 μm.

8.1. Relationships among colony size, cell abundance and colonial particulate organic carbon (POC)

Phaeocystis strains from the North Sea, western Norway, South Pacific and Ross Sea have shown a negative linear relationship between Log colonial cell abundance (cells per colony) and Log colony diameters, with a slope < 2 (Rousseau et al., 1990; Mathot et al., 2000; Jakobsen and Tang 2002; Verity et al., 2007; Wang et al., 2010), showing that the number of cells per unit surface area decreases as the colony size increases. Decreased colonial cell density with colony size implied that colony envelopes might become thinner and fragile, and restrict colony size, unless mucous material produced by colonial cells increases. A positive correlation between colonial cell density and colony diameter was found for giant colonies from Vietnamese waters, with a slope of 2.94, which was greater than all previous observations (Rousseau et al., 1990; Mathot et al., 2000; Jakobsen and Tang 2002; Verity et al., 2007; Wang et al., 2010). This relationship implies that colonial cells can supply greater amounts of carbon to build colonial envelopes, allowing colonies to grow larger. Based on the relationship between colonial cell density and colony diameter, the maximum colony size is predicted to be 9.77 cm (Liu, 2015). A weak but significant negative relationship was found between mucous POC per unit area of colony and colony size (Smith et al., 2014a), however, suggesting that carbon contributed by colonial cells failed to meet the demand of colony envelope as size increased. The mucous envelope becomes thinner as a colony grows larger, leading colonies to rupture due to the turbulent forces on the colony (Smith et al., 2014a; Wang et al., 2014).

8.2. Diffusive limitation of nutrient uptake

Another potential disadvantage of being large is nutrient availability, which could be limited both by diffusive boundary layers and the rates of flux across the envelope. The presence of diffusive boundary layers surrounding the colonies has been shown to limit nutrient uptake by *P. globosa* colonial cells, and the thickness of diffusive boundary layers increases with colony size (Ploug et al., 1999a). Mucous is a barrier to nutrient diffusion, although the *P. globosa* envelope appears to be permeable to oxygen diffusion (Ploug et al., 1999b). The envelop thickness of giant colonies of *P. globosa* in Vietnamese waters is *ca.* 50 μm, and the diffusion coefficients of ions across the mucous envelope of colonies with 1.0 cm diameter are $1.0 \pm 0.3 \times 10^{-7}$ cm^{-2} s^{-1}, which are10-fold lower than coefficients observed in seawater (Smith et al., 2014a). Colony formation and enlargement indeed restrict the movement of flux of ions, as well as presumably the nutrients availability for colonial cells, although cells are likely to uptake nutrients within mucilaginous matrix (Lancelot and Mathot 1987; Wang et al., 2014). As the colony grows larger, nutrient limitation results in decreased amount of carbon allocated to mucous envelop if individual cells are to maintain cell mass and growth rate, explaining the negative relationship between mucous POC per unit area of colony and colony size for giant colonies.

8.3. Sinking rates

Giant colonies have higher sedimentation rates relative to small colonies (Peperzak et al., 2003; Smith et al., 2014a); . *P. globosa* colonies in the Dutch coastal zone of the North Sea have shown various sinking rates ranging from −0.37 to 1.92 m d^{-1} (Peperzak et al., 2003), suggesting that colonies are capable of regulating buoyancy in the seawater (Wang and Tang 2010). Sinking rates of giant colonies collected from the Vietnamese waters ranged from 29.3 to 516 m d^{-1} (average of 189 m d^{-1}; Smith et al., 2014a). The high sinking rates pose a significant challenge for giant colonies to maintain their position in the euphotic zone, and may constraint the occurrence of blooms of giant colonies to shallow near-shore waters, where colonies can be re-suspended, allowing colonial cells to absorb light for photosynthesis. For example, strong northeast monsoon in winter breaks down stratification that formed in summer and results in the deep mixing (Bauer et al., 2013), which not only supply nutrient from the bottom to the surface, but also can re-suspend colonies to surface, contributing the occurrence of colonial *P. globosa* blooms in the Beibu Gulf.

Despite of the disadvantages of large sizes, giant colonies provide protection for cells embedded within colonies: colonies are less susceptible to being grazed by zooplankton due to toughness of the mucous envelope and the large colony size, thereby creating a size mismatch problem for grazers (Hamm et al., 1999; Jakobsen and Tang, 2002). The major advantage of colony formation and size increase appears to be the ability to escape grazing pressure, thereby reducing the population losses (Nejstgaard et al., 2007). Colony formation in *Phaeocystis* could be the result of a balance among avoidance of herbivory, removing available nutrients, growth and maintaining colony integrity.

9. Adaptation to local environments

The composition, distribution, and function of phytoplankton are the result of interactions of various internal and external factors that are responsible for growth and mortality (Boyd, 2002; Smetacek et al., 2004). Facing diverse competitors and herbivores as well as multiple environmental stresses, a species must maximize its reproductive rate while minimizing losses in order to bloom. The success of *Phaeocystis* in global ocean ecosystems is attributed mainly to their ability to form colonies, which decreased loss rates due to zooplankton grazing (Hamm et al., 1999, Nejstgaard et al., 2007). However, there is growing evidence that *Phaeocystis* can outcompete their competitors (e.g., diatoms) by adapting and acclimating to environments that are unfavorable for diatoms, as well as utilizing alternative resource. For example, diatoms were replaced by *P. globosa* at high temperature and high light (Jahnke, 1989; Peperzak et al., 1998). Although diatoms have higher rates of nitrate uptake than *Phaeocystis*, the latter increased ammonium uptake rates (Tungaraza et al., 2003), allowing *Phaeocystis* to outgrow diatoms when nitrate becomes limiting (Sanderson et al., 2008; Bradley et al., 2010; Wang et al., 2011; Smith, 1993). *P. antarctica* photosynthesize and grow at relatively low photon flux densities due to vertical mixing of the water column and ice cover (Moisan et al., 1998; Kropuenske et al., 2009; Smith and Asper., 2001). These abilities enable *Phaeocystis* to outgrow competitive species and dominate phytoplankton assemblages in certain marine systems. *P. globosa* in Chinese waters also showed flexible strategies to adapt and acclimate to local environments.

9.1. Blooms at higher temperature

Temperature is a fundamental environmental factor responsible for growth, elemental composition, photosynthesis, and distribution of *Phaeocystis* (Jahnke 1989; Peperzak et al., 2003; Schoemann et al., 2005; Wang et al., 2010). *P. globosa* generally blooms in temperate waters when temperature was <15 °C (Seuront et al., 2006; Blauw et al., 2010). The growth temperature range for *P. globosa* in culture was 2 to 30 °C, with optimal temperature of 15–20 °C (Jahnke and Baumann 1987; Schoemann et al., 2005). In contrast, *P. globosa* in the South China Sea can tolerate warmer temperatures. Most *P. globosa* blooms occurred in Chinese coastal waters when temperatures were 16–22 °C (Table 1), and experimental evidence showed that temperatures from 20–24 °C appear to be optimal temperature of growth and colony formation of *P. globosa* (Xu et al., 2017). However, *P. globosa* blooms also occur in the warmer waters. The bloom in Zhelin Bay in 1999 occurred when temperatures reached 26 °C (Chen et al., 1999; Xu et al., 2003), while *P. globosa* dominated in northeast Beibu Gulf in August through October, at which time temperatures ranged from 27.2 to 30.5 °C (Liu et al., 2008). *P. globosa* in culture could develop colonies at 30 °C (Tian and Lv., 2010), and survive at 35 °C in solitary form (Xu et al., 2017). The ability to develop colonies at higher temperatures explains the occurrence of colonial *P. globosa* blooms in the tropical coastal waters (Wang et al., 2010).

9.2. Nitrogen utilization

There is agreement that recurrent blooms of *Phaeocystis* colonies are controlled mainly by nitrate supply. Nitrate removal has been repeatedly observed during *Phaeocystis* blooms in North Pole, temperate seas and Antarctica waters (Lancelot and Mathot, 1987; Smith et al., 1998; Lancelot et al., 2007). Mesocosm experiments showed that the addition of nitrate induced *Phaeocystis* blooms, and that blooms collapsed once nitrate has been depleted (Sanderson et al., 2008; Bradley et al., 2010). *P. globosa* from South Pacific and North Atlantic waters developed colonies only with nitrate as the sole nitrogen source, while ammonium and urea supported growth of solitary cells rather than colonial cells (Wang et al., 2011). However, *P. globosa* in Chinese waters can develop colonies when nitrate and organic nitrogen are available. *P. globosa* from the Beibu Gulf developed colonies when nitrate was the sole nitrogen source (Liang et al., 2018). *P. globosa* could grow on ammonium (Meng et al., 2018), but only in solitary form (Liang et al., 2018). Ammonium is likely inhibitory to reproduction as well as allocation of carbon for colonial cells due to the redox imbalances and a surplus of reducing agents when ammonium was supplied as sole nitrogen source (Gilbert et al., 2016). *P. globosa* developed colonies and showed higher growth rates and cell abundances when grown on urea relative to nitrate (Qin et al., 2012; Liang et al., 2018; Meng et al., 2018). Urease, an enzyme responsible for the catabolism of urea, is likely to be active in *P. globosa* from Chinese waters, but inactive or absent for *P. globosa* observed elsewhere. When nitrate is limiting, it's possible that *P. globosa* maintains colonial cells to grow, reproduce, form greater colonies and persist bloom by utilizing urea as alternative nitrogen source. Urea have been a significant nitrogen source in the South China Sea (Zhang et al., 2020c; Yang et al., 2020), and the ability to utilize urea may contribute to the long-lived blooms of *P. globosa* observed in Chinese waters (Chen et al., 1999; Qi et al., 2004).

9.3. Light and darkness

Irradiance has been considered as one of the most important triggers to *P. globosa* blooms in the North Sea (Peperzak et al., 1998; Gypens et al., 2007; Blauw et al., 2010). *Phaeocystis* blooms developed when water column irradiance exceeded 25–35 μmol photons m^{-2} s^{-1} (Peperzak et al., 1998; Blauw et al., 2010). *Phaeocystis* in cultures developed colonies if irradiance daily exceeds the daily threshold of 100 W h m^{-2} (instantaneous light intensity of ~38 μmol photons m^{-2} s^{-1} if L:D ratio of 12:12 was considered), otherwise it only exists as solitary forms (Peperzak 1993). The growth and colony formation increased with irradiance levels, with maximum colony abundance at irradiance of 260 μmol photons m^{-2} s^{-1} (Peperzak, 1993). Although *in situ* investigations on the effects of irradiance on *P. globosa* blooms in Chinese waters are missing, the longer day length and higher solar irradiance in the South China Sea relative to the North Sea (Bauer et al., 2013; Gypens et al., 2007) suggests *P. globosa* can bloom at higher irradiance than *P. globosa* in the North Sea. There is experimental evidence indicating that *P. globosa* from Shantou coastal waters failed to develop colonies when irradiance was less than 50 μmol photons m^{-2} s^{-1}, but formed colonies of >400 colonies ml^{-1} with irradiance of 500 μmol photons m^{-2} s^{-1} (Wang et al., 2013), further suggesting that *P. globosa* from the South China Sea have adapted to higher irradiance condition.

Darkness is an important factor in maintaining bloom dynamics, because processes of DNA synthesis and cells division for *Phaeocystis* occur from late afternoon to midnight (Jacobsen and Veldhuis, 2005). Colony abundances and fraction of cells in colonial form for *P. globosa* collected from Shantou were suppressed when exposed to continuous light, while growth rates of colonial cells increased with dark periods (Wang et al., 2014). The nutrients (Fe and Mn) and energy stored in mucus matrix are likely to play a key role in facilitating the growth of colonial cells in darkness (Lancelot and Mathot, 1987; Schoemann et al., 2001).

9.4. Toxin and allelopathy

Many phytoplankton produce substances that negatively influence growth and behavior of co-occurring organisms (Ianora and Miralto, 2010; Turner, 2014). *P. globosa* cultures and extracts resulted in the mortality of *Epinephelus akaara* larval and shrimp *Penaeus vannamei*, while the motion of zooplankton *Artemia sinica* and *Brachionus plicatilis* was inhibited when *P. globosa* were supplied as sole food source (Shang, 2006). *E. akaara* larvae died once exposed to cell-free filtrate of *P. globosa* (Shang, 2006). Chemical analysis of wild *P. globosa* strains identified many toxic substances, which may be responsible for the mortality (Liu et al., 2010). Toxic substances from *P. globosa* that caused hemolysis of rabbit erythrocytes have been identified as glycolipids with a major digalactose and heptadecadienoyl group (He et al., 1999; Peng et al., 2005). These substances can combine its lipophilic groups with membranes of erythrocytes and destroy membrane structure by penetrating the phospholipid bilayer (Liu et al., 2007). High temperatures and irradiance levels enhanced the haemolytic activity of *P. globosa* (Guo et al., 2007; Liu et al., 2006), similar to the observations of Van Rijssel et al. (2007). The haeomolytic activity of *P. globosa* may explain the massive aquaculture and fishing losses associated with *P. globosa* blooms (Qi et al., 2004; Chen et al., 1999).

Phaeocystis have been suspected to inhibit the growth of other phytoplankton by releasing allelopathic compounds (Hansen et al., 2007). The growth of two bloom-forming dinoflagellate species was markedly reduced when co-cultured with *P. globosa* cell and their cell-free filtrates (Liu et al., 2010). Haemolytic compounds excreted from *P. globosa* are likely to be responsible for the inhibitory effect on dinoflagellates (Liu et al., 2010). Allelopathy of *P. globosa* on diatoms can contribute to *Phaeocystis* growth before diatom blooms even when Si is sufficient.

10. Mitigation of *P. globosa* blooms

The only practical method for mitigating *P. globosa* blooms has been the modified clays developed by scientists at the Institute of Oceanology of the Chinese Academy of Sciences (Yu et al., 2017). This method has been successfully developed and applied. Through analyzing the effect of six different aluminum-modified clays on mitigating *P. globosa* blooms, a strategy for achieving best removal efficiency was achieved, including decreasing the pH of modified clay suspension, enhancing the surface positive charge, and selecting an appropriate clay particle size (Cao et al., 2017; Qiu et al.,2020).

11. Conclusions and future perspectives

In the past 20 years, the morphology, structure, and life cycle alternation of *P. globosa* as well as various environmental factors regulating *P. globosa* blooms in Chinese coastal waters have been documented. Our analysis suggests that: (1) *Phaeocystis* blooms occurred after diatom blooms in the South China Sea, which is in agreement with observed phytoplankton succession during spring blooms in the North Sea. The diatom/*Phaeocystis* blooms could be a result of excess N and P load and consequently shift in nutrient ratio. (2) *P. globosa* blooms occurred typically in winter and in coastal waters of the South China Sea with strong northeast winds resulted in deep mixing and nutrients supply. Temperature and irradiance were at their annual minima, which are favorable to the onset of blooms. (3) The ability of *P. globosa* to utilize organic nitrogen may favor colonies to grow large and extend blooms periods when nitrate has been depleted. (4) *P. globosa* seems to have adapted to higher temperature and light, allowing blooms to occasionally occur in summer and fall in the South China Sea. Compared with *P. globosa* in the North Sea, *P. globosa* from the South China Sea showed some unique morphological features: relatively smaller solitary and colonial cells, unequal flagella as well as the largest colonies in the world. (5) Giant colonies exhibited enhanced sinking rates and decreased mucous carbon per unit of colony surface with size. Some of these findings are consistent with *P. globosa* in the Atlantic and suggested that a similar environmental factor regulating these blooms existed in both Europe and China. Certain unique survival strategies that were different with those previous known in elsewhere contribute *P. globosa* to adapt and bloom in Chinese waters.

However, current knowledge of ecology and biology of *P. globosa* in China waters is still incomplete. Investigations on the relationship between *Phaeocystis* blooms and environmental factors, including nutrients, light, temperature, wind and vertical mixing, as well as biological factors (e.g., interactions with bacteria, diatoms, and zooplankton) are limited and prevent us from understanding the mechanisms underlying the blooms. In addition, the impact of *Phaeocystis* blooms on transfer of carbon and sulphur between ocean and atmosphere remains unknown. Finally, the role of *P. globosa* blooms in nutrient remineralization within the microbial web, trophic efficiency, and function and structure of marine food webs also remain uncertain. Empirical studies and model interpretation are need to address these questions, allowing marine scientists to gain deeper insights into the biology, ecology and biogeochemistry of *Phaeocystis*.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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